AN ANALYSIS OF THE CRANIAL GANGLIA OF AN EMBRYO SALAMANDER, AMBYSTOMA JEFFERSONIANUM (Green).

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INTRODUCTION.

Since the pioneer work of Strong (1895) on the nerve components of the cranial nerves of Amphibia, a number of other papers have appeared dealing with the composition of these nerves in various members of the same group. Most of these studies have dealt with various species of urodeles, and have been concerned more particularly with the peripheral distribution of the nerves in the adult or late larval forms.

In these late larval and adult stages the ganglia of the cranial nerves are invariably more or less fused, forming in the Anura two, in the Urodela usually three, general ganglionic masses. In consequence of this fusion, the fundamental relations of the individual ganglia are largely obscured, and the analysis of these ganglionic masses into their component parts is made exceedingly difficult and oftentimes impossible.

The importance of studying early embryonic stages in which the fusion spoken of above has not yet taken place, and in which, therefore, the primary relations of the ganglia still obtain, was emphasized by Landacre and McLellan's analysis of the cranial ganglia of the embryo of Rana (1912). The present paper is offered as an attempt to analyze, by the use of similar methods, the cranial ganglia of an embryo urodele.

Material.

Except where otherwise stated, the descriptions, drawings, and reconstructions which follow are from a single embryo of Ambystoma jeffersonianum (Green), 11.5 mm. in length. This embryo was killed about nineteen days after fertilization, most of the development having taken place in a room where the temperature was mild and fairly constant. Most of the remaining embryos of the same egg mass hatched six days later. A considerable number of other specimens, some younger and some older than the 11.5 mm. embryo, were also studied and the conclusions reached from the study of the latter were thus checked up.

It was found that considerable variation in position and in degree of fusion between the ganglia was present in embryos of approximately the same age. Even the two sides of the same individual often presented considerable differences. Nevertheless, the more general relations between the ganglia and between these and their roots and rami were found, on the whole, to remain constant. Likewise, while the degree of fusion between given parts might be considerably less in some older individuals than in certain younger ones, there was found to obtain in general a definite progression from the free to the fused condition paralleling the progression from early to late stages. The 11.5 mm. embryo described was selected because it showed what seemed to be, on the whole, the most typical condition for that stage.

The material was killed and fixed in Zenker's fluid, and after sectioning was stained with Delafield's hæmatoxylin and orange G. The studies were made almost entirely from transverse sections 10 microns in thickness, though two specimens cut into parasagittal sections of the same thickness were also used.

For this material, and for numerous suggestions and criticisms as well, I wish to acknowledge my deep obligation to Professor F. L. Landacre.

Scope and Methods.

While the cranial ganglia in the 11.5 mm. embryo are more crowded together than in earlier stages, and a certain amount of fusion has already taken place, this embryo was chosen for detailed study and reconstruction because of the much more complete development of the nerve trunks and their branches. This made possible certain identification of the various ganglia, which was the main object of the present investigation. However, a detailed study of the distribution of the nerves was not attempted; and only as much of this distribution is given in the following description as seems necessary to establish the character of the several ganglia. For the sake of clearness and simplicity, the distribution of the nerves is not included in the reconstruction. For the same reason, while all motor components that were definitely identified as such are described in the text, these have been omitted from the reconstruction.

The lateral view reconstruction shown in Plate I was made by the ordinary method of projecting, by means of a camera lucida, sections magnified to a definite size upon coordinate paper, and plotting the upper and lower limits of the various structures in consecutive sections. The reconstruction is thus a projection of these structures upon the sagittal plane.

The nomenclature used has been, as far as possible, the same as that of Coghill (1902), whose thorough and painstaking description of the cranial nerves in the late larval stage of Ambystoma tigrinum was found of great assistance. To some extent, however, I have made use of the nomenclature of Landacre and other authors.

General State of Development of the 11.5 mm. Embryo.

In the 11.5 mm. embryo of Ambystoma jeffersonianum the general relations of the parts of the central nervous system are already essentially the same as in the adult, though the brain is comparatively shorter antero-posteriorly, and the cephalic flexure is more marked. The cranial ganglia are readily recognizable, and their roots and principal trunks and rami are for the most part well defined. In the preparations studied no trace of myelination of the fibers can as yet be detected; though usually numbers of elongated cells (the future sheath-cells) are strung along the bundles of fibers. A root or ramus when cut in cross-section often shows the nuclei of some of these cells in among the fibers. In many cases fibers can be traced directly to the muscles, sense-organs, or other tissues which they innervate; but for the most part this is very difficult, owing to the absence of myelination and the obscuring presence of numerous yolk-laden mesenchyme cells.

At this stage of development the differences in size and staining reaction between the fibers of different components, reported by various writers, are not observable; except that when, as is rarely the case, isolated fibers are found, those from lateralis ganglia appear to be slightly larger than those from other ganglia.

The auditory vesicle, in the embryo here described, is in an early stage of the formation of the semi-circular canals; the septa of the lateral and anterior canals have just been formed, while that of the posterior canal is represented as yet only by an infolding of the lateral wall of the vesicle, which fold projects mesio-ventrad into the cavity of the latter. (Norris, 1892).

Lateral line organs are numerous on the side of the head, and readily recognized.

The skeletal system is in a very early stage of development. The chondrocranium is as yet represented only by the parachordals and the trabeculæ, which at this time are little more than narrow bars. The visceral arches (branchial bars) are fairly well defined. The palatoquadrate cartilages are not as yet fused with the trabeculæ. All these structures are in a very early stage of chondrification. Actual chondrification of the auditory capsule has not as yet commenced, though an organization of mesenchyme about the vesicle, preparatory to chondrification, is already apparent.

The pharynx is still closed anteriorly at this stage. Gill clefts have not yet appeared, but their future position is indicated by endodermic outgrowths from the wall of the pharynx to the spaces between the external gills. The breaking open of the mouth and that of the gill clefts seem to take place nearly at the same time, and but little later than the stage described.

The Ganglia of the V (Trigeminus), VII (Facialis), and VIII (Auditory) Nerves.

The ganglia of the V, VII, and VIII nerves fall distinctly into two groups. The Gasserian and dorsal lateralis VII ganglia comprise the more anterior group; the geniculate, ventral lateralis VII, and auditory ganglia comprise the more posterior. This grouping is not, however, as striking a feature as it seems to be in some of the late larval forms hitherto described, the anterior border of the geniculate ganglion, for example, being barely 10 microns posterior to the most posterior portion of the Gasserian (Plate I). Later in the development (in the young larva) the lengthening of the head brings with it an increase in the distance between these ganglia; and the work of Coghill (1902) shows that this tendency becomes even more marked in the late larval stages.

Cutaneous V or Gasserian Ganglion.

The Gasserian ganglion, at this stage, is readily recognized as a rather large mass of cells, somewhat oblong in cross-section, and pressed close to the lower portion of the side of the medulla at the anterior end of the latter (Plate I, *G. Gass.* + *Prof.;* Plate II, Fig. 1, *G. Gass.;* Plate IV, Fig. 1a). Its anterior portion extends for a short distance into the region between the brain and the optic vesicle; its posterior part for a shorter distance into that between the brain and the auditory vesicle. Its ventro-lateral portion is in contact with the anterior extremity of the palatoquadrate bar (Plate II, Fig. 1; Plate IV, Fig. 1a).

At this stage no distinction can be made out with certainty between the profundus portion and the Gasserian proper portion of the ganglion. In considerably earlier stages, however, this distinction is very marked, the profundus portion projecting forward for a considerable distance above the optic vesicle. In these earlier stages both portions of the ganglion lie much closer to the ectoderm of the side of the head.

In its posterior part the dorsal portion of the Gasserian ganglion is in close contact with the dorsal lateralis VII ganglion (Plate I, and Plate II, Fig. 1, *G. D. L. VII*). The two are readily separated, however, because of the histological differences between them. (See p. 251; also Plate IV, Fig. 1a).

The root of the Gasserian ganglion leaves its dorso-mesial surface near the center of its posterior half. (See Plate I, dotted lines, and Plate II, Fig. 1, *Rt. Gass.*; also Plate IV, Fig. 1a). It is exceedingly short, entering the medulla at a point directly opposite its point of exit from the ganglion. In older stages the root becomes considerably longer, and runs caudad for some distance before entering the medulla; this is the condition which has been uniformly reported for late larval stages in urodeles.

Three rami arise from the Gasserian ganglion. The *ramus ophthalmicus profundus V* (Plate I, *R.O.P. V*) arises from its most anterior portion; it dips at first rather suddenly downward for a short distance, and then takes its course forward between the brain and the optic vesicle.

The *ramus maxillaris V* (Plate I, *R. Mx. V*) arises from the dorso-lateral part of the ganglion, at a transverse level nearly at the middle of the ganglion. It at once unites with the ramus buccalis VII to form the infra-orbital trunk, which takes its course at first latero-ventrad and a little forward, and then more directly forward between the optic vesicle and the skin, close to the outer surface of the former.

The *ramus mandibularis V* (Plate I; Plate II, Fig. 1; Plate IV, Fig. 1a; *R. Mnd. V*) leaves the lateral portion of the ganglion a few sections posterior to the origin of the ramus maxillaris, and at a point directly dorsal to the palatoquadrate bar. It runs at first latero-ventrad and then almost directly ventrad between the temporalis and masseter muscles to the region of Meckel's cartilage. The further course of its principal portion is in general cephalad. Fibers from it were traced directly to the undifferentiated ectoderm, below Meckel's cartilage, helping thus to confirm the general cutaneous character of the ganglion.

Motor component V. In the postero-ventral portion of the root of the Gasserian, a bundle of fibers may be recognized as a motor component because of the fact that its fibers, unlike the rest, after entering the medulla run down into its ventral horn. These fibers pass directly through the ganglion, emerging with and as a part of the ramus mandibularis, in which they occupy a postero-ventral position. A short distance beyond the ganglion a portion (at least) of these fibers is given off from the ventral side of the ramus mandibularis, and innervates the temporalis muscle, thus confirming the motor character of this component.

Dorsal Lateralis VII Ganglion.

Throughout most of its length this ganglion appears in cross-section as a more or less rounded or oblong mass dorsal to the Gasserian, to which for some distance it is closely pressed (Plate I; Plate II, Fig. 1; Plate IV, Fig. 1a; *G. D. L. VII*). Nevertheless, as stated above, the two can be readily distinguished. Its posterior portion extends backward between the auditory vesicle and the medulla, and gives rise to its root at a transverse level but little farther caudad than that of the posterior end of the Gasserian. This root, owing to the narrow space between the ear and the medulla through which it passes, is much compressed from side to side, giving it, in the reconstruction, a false appearance of great bulk (Plate I, *Rt. D. L. VII*). The root continues backward to its junction with the root of the ventral lateralis VII ganglion (Plate I; Plate II, Fig. 2; Plate IV, Fig. 2a). Slightly posterior to this junction the combined roots enter the medulla. This point of entrance is at a horizontal level much higher than that of the root of the Gasserian. (Plate I, dotted lines; also Plate II, Fig. 3, *Rt. D. + V. L. VII*).

The *ramus ophthalmicus superficialis VII* (Plate I, *R. O. S. VII*) leaves the dorsal lateralis VII ganglion at its anterior end. It passes forward and somewhat dorso-laterad for a considerable distance, running directly above the eye. Branches from it were traced to the lateral line organs of this region. No evidence was found of any other component in this ramus.

About four sections (40 microns) farther back the *ramus buccalis VII* (Plate I, *R. Bu. VII*) leaves the ventro-lateral portion of the ganglion, and at once joins with the cutaneous ramus maxillaris V to form the infra-orbital trunk. At the point where the two unite, a branch is given off posteriorly (Plate I; Plate II, Fig. 1; Plate IV, Fig. 1a; *R. Bu. VII, 1*) which runs ventro-laterad and for a short distance back around the anterior end of the auditory vesicle. Its fibers were traced to lateral line organs in this region. The general course of the main portion of the infra-orbital trunk has been given above (p. 235). Fibers from it were traced to numerous lateral line organs.

Ventral Lateralis VII Ganglion.

This, the farthest ventrally of all the ganglia here described, is a spindle-shaped mass of cells lying ventral to the anterior portion of the auditory vesicle (Plate I; Plate II, Figs. 2 and 3; Plate IV, Figs. 2a and 3a; *G. V. L. VII*). Its long axis is directed ventro-laterad and slightly caudad. Its proximal end is well fused with the distal portion of the geniculate ganglion, although, as in the case of the dorsal lateralis VII and Gasserian ganglia, the boundary between the two is readily recognized. The distal end of the ganglion lies upon and in contact with an outgrowth of endoderm which projects dorsad from the lateral angle of the pharynx in this region (Plate II, Figs. 2 and 3; *En.*).

The root of the ventral lateralis VII ganglion is comparatively long (Plate I; Plate II, Fig. 2; Plate IV, Fig. 2a; *Rt. V. L. VII*); as it runs mesio-dorsad to its junction with the root of the dorsal lateralis ganglion, it is pressed between the geniculate ganglion, the auditory vesicle, and the anterior border of the auditory ganglion.

But one ramus arises from this ganglion, the *ramus mentalis VII* (Plate I; Plate II, Fig. 3; Plate IV, Fig. 3a; *R. Mnt. VII*). This component of the hyomandibular trunk leaves the distal extremity of the ganglion; it passes, just posterior to the articulation of Meckel's cartilage with the palatoquadrate bar, abruptly ventrad and lateral to the hyoid bar. When close to the ectoderm in the ventro-lateral region of the head it turns forward, supplying lateral line organs in this region and farther cephalad. A short distance from the ganglion it gives off a lateral branch which passes directly to the skin and likewise innervates lateral line organs.

Visceral VII or Geniculate Ganglion.

The geniculate ganglion (Plate I; Plate II, Figs. 2 and 3; Plate IV, Figs. 2a and 3a; *G. Gen.*) is directly posterior to the Gasserian, and in the 11.5 mm. embryo it almost touches the posterior border of the latter. In its anterior portion it is roughly wedge-shaped as seen in cross-section, the point of the wedge extending dorsad between the medulla and the ear (Plate II, Fig. 2; Plate IV, Fig. 2a). Posteriorly the ganglion is pressed close against the antero-mesial surface of the auditory ganglion, the anterior end of which is introduced between the geniculate ganglion and the ear (Plate II, Fig. 3; Plate IV, Fig. 3a; *G. Aud.*). This contact between the two ganglia is very close, and in some specimens it is very difficult to distinguish the exact boundary between the two.

The root of the geniculate ganglion (Plate I; Plate II, Fig. 3; Plate IV, Fig. 3a; *Rt. Gen.*) arises from its postero-dorsal portion; it passes dorsad and caudad for a short distance, pressed close to the mesial surface of the auditory ganglion, and enters the medulla at a horizontal level lower than the lateralis root of VII, yet somewhat higher than the root of the Gasserian. The area of entry is but two or three sections (20 or 30 microns) farther caudad than that of the lateralis root.

Two rami arise from the geniculate ganglion. The *ramus alveolaris VII*, the visceral component of the hyomandibular trunk, leaves the ventro-lateral portion of the ganglion, directly underneath the proximal end of the ventral lateralis VII ganglion (Plate I, *R. Alv. VII*). It proceeds parallel to the long axis of this latter ganglion, in close contact with its ventral surface (Plate II, Fig. 3; Plate IV, Fig. 3a), and soon turns abruptly ventrad, running parallel and mesial to the ramus mentalis, but quite distinct from it. At about the horizontal level of the middle of the pharynx it turns forward and runs cephalad. When traced forward it is soon lost, its fibers apparently ending in the epithelium of the pharynx.

The *ramus palatinus VII* (Plate I, *R. Pal. VII*) leaves the antero-ventral portion of the ganglion and inclines cephalo-ventrad. Its fibers also end in close relationship with the epithelium of the pharynx.

Auditory Ganglion.

The auditory ganglion (Plate I; Plate II, Figs. 3 and 4; Plate IV, Figs. 3a and 4a; *G. Aud.*) lies between the ventral portion of the auditory vesicle and the medulla, and throughout most of its length is in contact with the former. Its anterior portion is wedged in between the ear and the geniculate ganglion (Plate II, Fig. 3; Plate IV, Fig. 3a), and its anterior-most border is in contact with the root of the ventral lateralis VII ganglion. Its dorso-ventral extent is much greater anteriorly than farther back, reaching from a level below the base of the medulla to a level just above the area of entry of the root of the geniculate. Posteriorly it tapers, somewhat more rapidly on its upper surface, and reaches as far as the posterior third of the auditory vesicle.

The only root of the auditory ganglion recognized with certainty as such leaves its dorso-mesial portion, and, passing slightly caudad and dorsad, enters the medulla in contact with and ventro-posterior to the root of the geniculate (Plate I, *Rt. Aud.*). It is in even closer relationship with the motor root which leaves the medulla just ventral to it; the exact limits of these roots are very hard to distinguish.

Coghill describes two auditory ganglia, a vestibular and a cochlear, each with its own root, in the late larval stage of Ambystoma. Norris finds two auditory roots in Amphiuma, but does not distinguish two distinct ganglia, merely recognizing vestibular and cochlear portions of one auditory ganglion. In the embryo here described it has likewise been impossible to distinguish two distinct ganglia. In young larval stages considerably older than the 11.5 mm. embryo, two different regions, one more anterior and dorsal, the other more posterior and ventral, may be identified. These regions are characterized by histological differences (p. 252), but no definite boundary between them can be determined. In the 11.5 mm. embryo the beginnings of this histological differentiation can be just barely recognized, and the transition in structure from one portion of the ganglion to the other is even more gradual than in later stages.

Only two rami from the auditory ganglion, both of them small and unbranched, are present in the 11.5 mm. embryo. The larger and more anterior of these (Plate II, Fig. 3; Plate IV, Fig. 3a; *R. Utr. VIII;* not shown in reconstruction) arises from the ventro-lateral portion of the ganglion, near its anterior end, and passes laterad in close contact with the ventral surface of the auditory vesicle to the macula of the utriculus; a few of the fibers appear to pass beyond to the crista of the horizontal canal. The smaller and more posterior ramus (Plate II, Fig. 4; Plate IV, Fig. 4a; *R. Sac. VIII;* not shown in reconstruction) arises from the postero-lateral portion of the ganglion and passes laterad to the macula of the sacculus. These small rami are undoubtedly the incipient *ramus acusticus utriculi* and *ramus acusticus sacculi* respectively.

Motor component VII. Immediately ventral to the area of entry of the auditory root a bundle of motor fibers emerges from the medulla. The character of this component is indicated by the course of the fibers within the medulla, where they are readily traced to the ventral horn, and is confirmed by their peripheral distribution. The component extends ventro-laterad, pressed close between the auditory and geniculate ganglia (Plate II, Fig. 3; Plate IV, Fig. 3a), and as it emerges from between them it comes to lie on the posterior surface of the ventral lateralis ganglion. Thence it continues ventro-laterad for a short distance, and its fibers enter the depressor mandibulæ muscle. At all points its fibers are quite distinct from those of the remainder of the hyomandibular trunk.

The Ganglia of the IX (Glossopharyngeus) and X (Vagus) Nerves.

At the stage of the 11.5 mm. embryo the ganglia of the IX-X complex are in a condition intermediate between the earliest stage of well-defined and almost entirely separate ganglia and the later stage of complete fusion into one ganglionic mass. The ganglia are already crowded together, and to some extent actual fusion has taken place. For the most part, however, the limits of the individual ganglia are readily discernible.

In the more general relations of its parts this group bears a distinct resemblance to the same complex in the embryo of Rana, as reported by Landacre and McLellan. The visceral ganglia—visceral IX, or petrosal, and visceral X, or nodosal—are ventral in position; the one cutaneous ganglion—cutaneous X, or jugular—more dorsal and mesial; while the lateralis ganglia, present, as in Rana, in both IX and X, occupy a position dorsal and lateral to the other ganglia of the complex.

The roots of these ganglia enter the medulla in three distinct areas. Of these, the most anterior is that of the one lateralis root of the complex, composed of all the lateralis root fibers from both IX and X. Slightly caudad and ventrad of this enters the root of the visceral IX ganglion; and considerably farther back the roots of the visceral X and cutaneous X ganglia enter together.

These relations are essentially the same as those described by Coghill for the late larval stage of Ambystoma, except that he describes two roots for visceral X, entering the medulla separately. This I have not been able to demonstrate in the 11.5 mm. embryo, nor in any of the other stages at hand. All the visceral root fibers from X apparently enter the medulla together.

Visceral IX or Petrosal Ganglion.

The most anterior of the ganglia of the IX-X complex is the visceral IX (G. petrosum). (Plate I; Plate III, Figs. 5, 6, and 7; Plate IV, Figs. 5a, 6a, and 7a; *G. Vi. IX*). It lies immediately posterior to the auditory vesicle, its dorso-anterior portion extending mesial to the posterior extremity of the latter. In cross-section it is more or less oval in shape, and the long axis is inclined ventro-laterad.

The root of the visceral IX ganglion (Plate I, *Rt. Vi. IX*) arises from its antero-dorsal portion, and passes forward and mesio-dorsad for about eight sections (80 microns) before entering the medulla. The area of entry is ventro-posterior to that of the lateralis IX and X root; its horizontal level (with respect to the base of the medulla) is nearly the same as that of the root of the geniculate ganglion. Motor fibers were recognized in this root, in the same way as in the roots of V and VII, but I was not able to trace them through the ganglion.

The one nerve that leaves this ganglion, the *truncus glossopharyngeus IX* (Plate I; Plate III, Fig. 5; Plate IV, Fig. 5a; *T. Gl. IX*), arises from its ventro-lateral border and passes ventro-laterad and slightly cephalad to the region of the first branchial bar. A short distance beyond the ganglion a small branch (not shown in the reconstruction) is given off ventrally, and passes ventro-cephalad. It could not be traced very far, but apparently ends while in close relationship with the epithelium of the pharynx.

Just above the first branchial bar the glossopharyngeal trunk passes close to the first levator arcus branchialis muscle, and a portion of its fibers (motor component of IX) enter this muscle. The principal portion of the trunk turns cephalad, and extends in this general direction for a long distance, at first lateral to the first branchial bar, but gradually passing ventrad and mesiad; it finally ends in the epithelium of the basal portion of the tongue. It should be noted here that this is not the complete distribution of the glossopharyngeal trunk. As in the case of other trunks and rami, minor branches were not followed.

The *ramus communicans IX + X ad VII*, described by Coghill, Bowers, and Norris as present in the late larval stages of Ambystoma, Spelerpes, and Amphiuma respectively, could not be found in any of the embryos or young larvæ which I studied.

Coghill finds in the late larva of Ambystoma a cutaneous component in the truncus glossopharyngeus, apparently derived from the cutaneous X ganglion. This, again, I was not able to demonstrate in the material at hand.

Lateralis IX and X Root.

Before taking up any of the lateralis ganglia of IX and X, a few words regarding the common root of these ganglia (Plate I, *Rt. L. IX + X*) will prove helpful. The most posterior portion of this root arises from the dorsal lateralis X ganglion (Plate I, *G. D. L. X*), well back in the complex, and extends cephalad, for most of the distance dorsal to the cutaneous X ganglion (Plate III, Figs. 6, 7, and 8; Plate IV, Figs. 6a, 7a, and 8a; *Rt. L. X; G. Cu. X*) as far as the lateralis IX ganglia (Plate I; Plate III, Figs. 5 and 6; Plate IV, Figs. 5a and 6a; *G. D. L. IX* and *G. V. L. IX*). As it passes close to the mesial surface of the latter, the root fibers of these ganglia are added to it. Running dorsal to the visceral IX root, it continues cephalad, and now somewhat dorso-mesiad, to its area of entry into the medulla. This area is antero-dorsal to that of the visceral IX root, and is nearly at the same horizontal level as that of the lateralis roots of VII.

On one side of one individual, a radical variation was found, the lateralis root of X entering the medulla quite separate from that of IX, and a short distance farther caudad than the lateralis and visceral roots of IX. What significance, if any, this interesting variation may have, it is impossible to say; the mere possibility that it is a reversion to a more primitive condition naturally suggests itself.

Lateralis IX Ganglia.

In the earlier stages there are two distinct lateralis ganglia present in close relationship with the visceral IX ganglion. Each sends its own root to join the general lateralis root of IX and X. From the more anterior and ventral of these ganglia the ramus supratemporalis IX arises; from the more posterior and dorsal, the lateralis component of the ramus auricularis IX + X. These two ganglia usually soon fuse, to a greater or less degree, and in the 11.5 mm. embryo they appear as one continuous ganglion. (Plate I; Plate III, Figs. 5 and 6; Plate IV, Figs. 5a and 6a; *G. D. L. IX* and *G. V. L. IX*). The apparent bilobing of this ganglion in the reconstruction does not accurately represent this double condition, though roughly it does; the more ventral of the ganglia is represented by a portion of the upper lobe as well as all of the lower.

In some individuals of stages somewhat older than the 11.5 mm. embryo, and even in a few of that stage, the dorsal lateralis IX ganglion comes into close contact with the ventral lateralis X ganglion, forming with it a single, continuous mass of cells.

From a study of such cases alone it would be easy to infer that the two actually represent but a single ganglion, and that the lateralis component of the R. auricularis therefore arises from ventral lateralis X. Against this interpretation, however, must be placed the indisputable fact that the cell masses which form these two ganglia are uniformly quite distinct in the early stages, and in the greater number of cases remain distinct for a considerable time, even after the development of the nerves to which they give rise.

Because of the close relationship of both dorsal and ventral lateralis IX to the visceral IX ganglion, and because of their usual fusion with each other, it seemed best to place both these ganglia on IX. However, it seems quite possible that the ganglion identified as dorsal lateralis IX actually belongs primitively on X, and corresponds to the first of the three lateralis ganglia on X which Landacre has described in Squalus. Either interpretation is bound to be more or less arbitrary.

In the 11.5 mm. embryo the greater part of the combined lateralis IX ganglia lies directly above the visceral IX ganglion, and in contact with the lateral border of the lateralis IX and X root (Plate III, Fig. 5; Plate IV, Fig. 5a). The individual roots of both lateralis IX ganglia can be distinguished, though with great difficulty, as both are exceedingly short before they unite with the root of lateralis X.

The combined lateralis IX ganglia comprise a comparatively small mass of cells; the most ventral portion, as seen in transverse section, consists merely of a single or at most a double layer of cells pressed close to the dorso-lateral border of the visceral IX ganglion. The appearance of this ventral portion in the reconstruction is deceptive, its size as seen in the lateral view giving the idea of considerable bulk, which it does not possess. (Compare Plate I with Plate III, Figs. 5 and 6.) The cells of this ventral portion extend down toward the point of origin of the truncus glossopharyngeus, and in some specimens strongly suggest the idea that they may send lateralis fibers into this trunk. However, no such fibers could be traced with certainty; and as far as the distribution of the glossopharyngeal trunk was followed, no lateral line organs could be found to be innervated by its fibers.

The actual number of rami from lateralis IX seems to vary somewhat with the age. In the 11.5 mm. embryo there are three definite rami (Plate I; Plate III, Figs. 5 and 6; Plate IV, Figs. 5a and 6a; *R. Spt. IX;* and *R. Aur. 1, IX* and *R. Aur. 2, IX*) and one slight fibrous outgrowth which does not as yet extend far beyond the surface of the ganglion (Plate III, Fig. 5; Plate IV, Fig. 5a; *R. Aur. ?*, not shown in the reconstruction). A study of many individuals of various stages shows that these rami fall distinctly into two groups, each group arising from a different one of the two original ganglia of which lateralis IX is composed. The distribution of these two groups corresponds in a general way with that usually given for the ramus supratemporalis and ramus auricularis respectively. Moreover, the more posterior of these groups is almost invariably closely associated near its place of origin with a component from the cutaneous X ganglion, while the other is not. As this also agrees with the conditions of the two rami as reported in late larval stages of both Ambystoma and Amphiuma, there seems to be no doubt of the homology.

In the 11.5 mm. embryo the *ramus supratemporalis IX* (Plate I; Plate III, Fig. 5; Plate IV, Fig. 5a; *R. Spt. IX*) arises from the antero-lateral portion of the combined lateralis IX ganglia. It passes laterad and somewhat dorso-cephalad around the hind border of the auditory vesicle and innervates lateral line organs in the region of the posterior portion of the ear. Its subdivisions seem to vary in different individuals, but in most it shows two main branches, one more dorsal than the other.

The two rami which I have identified as lateralis components of the *ramus auricularis IX + X* (Plate I; Plate III, Fig. 6; Plate IV, Fig. 6a; *R. Aur. 1, IX* and *R. Aur. 2, IX + X*) arise from the dorso-lateral portion of the combined ganglia, a little farther caudad and considerably farther dorsad than the origin of the ramus supratemporalis. They arise together, the more anterior (*R. Aur. 1*) extending dorso-laterad and then a little cephalad. The other (*R. Aur. 2*) inclines more caudad; it unites at once upon leaving the ganglion with fibers from the cutaneous X ganglion, and runs latero-dorsad, and for a short distance caudad, to the ectoderm. Fibers from both these rami were traced to lateral line organs in the region just posterior to the ear.

Cutaneous X or Jugular Ganglion.

Of the four ganglia of X, the cutaneous X or jugular ganglion (Plate I, *Rt. G. Cu. X;* Plate III, Figs. 6, 7, and 8; Plate IV, Figs. 6a, 7a, and 8a; *G. Cu. X*) is closest to the wall of the medulla. It also extends the farthest forward, its anterior portion projecting cephalo-laterad between the dorsal lateralis IX, above, and ventral lateralis IX, together with visceral IX, below. (See Plate III, Fig. 6; Plate IV, Fig. 6a.)

As was stated above, the lateralis X root passes cephalad close to the dorsal surface of the cutaneous X ganglion; a small portion of the ganglion extends slightly dorso-mesial to this root (Plate III, Figs. 6 and 7; Plate IV, Figs. 6a and 7a). Lateral to the cutaneous ganglion lie the anterior portions of the ventral lateralis X and visceral X ganglia, the visceral X being crowded close against most of the lower portion of its lateral border (Plate III, Figs. 7 and 8; Plate IV, Figs. 7a and 8a). The limits of the two ganglia, are, nevertheless, readily distinguished.

The root of the cutaneous X ganglion (Plate I, *Rt. G. Cu. X;* Plate III, Figs. 6 and 7; Plate IV, Figs. 6a and 7a; *Rt. Cu. X*) arises from its dorso-mesial portion; it passes dorso-mesiad, in company with the root of the visceral X ganglion and a portion of the motor fibers of X, directly to the medulla. This combined cutaneous, visceral, and motor root is very thick. The horizontal level of its area of entry into the medulla, with reference to the base of the medulla, is somewhat lower than that of the Gasserian or geniculate roots; but since the height of the medulla at this point is considerably less than in the region of V and VII, relatively the level is approximately the same.

The only ramus from this ganglion that could be identified with certainty as such was the cutaneous component of the *ramus auricularis IX + X* (Plate I; Plate III, Fig. 6; Plate IV, Fig. 6a; *R. Aur. 2, IX + X*). This arises from the most anterior and lateral portion of the ganglion, just ventral to the posterior portion of the dorsal lateralis IX ganglion, and at once joins with the lateralis component from the latter. The two pass dorso-laterad and somewhat caudad to the ectoderm of the region just posterior to the ear. Some of the fibers were traced to undifferentiated ectoderm, confirming the cutaneous character of this component.

The cutaneous components found by Coghill in the glosso-pharyngeal trunk and in both branchial trunks in the late larval stage of Ambystoma, I was not able to demonstrate with certainty in my material.

Visceral X or Nodosal Ganglion.

In the earlier stages the visceral X ganglion (G. nodosum) (Plate I; Plate III, Figs. 7, 8, and 9; Plate IV, Figs. 7a, 8a, and 9a; *G. Vi. X*) shows a very evident division into two parts, the more anterior of these giving rise to the two branchial trunks, the posterior to the visceral trunk. The two portions are continuous with each other, the division between them being marked simply by a very decided constriction in the middle portion of the ganglion.

This division of the visceral X ganglion into two parts, a branchial and a visceral, was also found by Landacre and McLellan in the embryo of Rana. The possible homology of the anterior portion with one or more of the branchial ganglia of fishes is discussed by these authors. A comparison with the visceral ganglia of X in Menidia (Herrick, 1899) or Squalus (Landacre, 1916) strongly suggests the probability of such a homology.

In the 11.5 mm. embryo from which the reconstruction was made, the constriction between the two portions of the visceral X ganglion has disappeared, and the ganglion appears as a single large, elongated mass, which is somewhat larger in transverse extent in the region of the branchial trunks than farther back. In some specimens, however, this constriction persists to a much later stage of development.

Anteriorly the visceral X ganglion extends, together with the ventral lateralis ganglion just above it, for a slight distance latero-dorsal of the visceral IX ganglion. Its anterior third is in close contact with the lower portion of the lateral surface of the jugular ganglion. Throughout most of its extent, the lateralis X ganglia lie in close contact with its dorsal, and to some extent lateral, surfaces, as will be described below.

The root of the visceral X ganglion (Plate I; Plate III, Figs. 6, 7, and 8; Plate IV, Figs. 6a, 7a, and 8a; *Rt. Vi. X*) leaves its dorso-mesial surface, a little caudad of the posterior border of the cutaneous ganglion. It passes, at first pressed close to the posterior surface of the latter ganglion, dorso-mesiad and somewhat cephalad to the medulla, which it enters in company with the cutaneous root and a portion of the motor root of X.

The visceral components of the two *branchial trunks* (Plate I; Plate III, Fig. 8; Plate IV, Fig. 8a; *T. Br. 1, X* and *T. Br. 2, X*) leave the ganglion close together. They arise from its ventro-lateral border, not far from its anterior end, the place of origin of the second branchial trunk being usually just posterior to that of the first. The course of the first of these is in general ventro-laterad and somewhat caudad; that of the second is similar, but more caudad.

A short distance beyond the ganglion a ventral branch (not shown in the reconstruction) leaves the first branchial trunk; it inclines ventro-caudad and soon disappears in contact with the epithelium of the pharynx. This is evidently the "pharyngeal ramus, 1 br. 1," of Coghill (1902, Plate XVI).

On their way to the periphery, both branchial trunks come into close relations with certain small gill muscles (not identified); and it appears quite probable that motor fibers present in these trunks are given off to these muscles, as Coghill found to be the case in the late larval stage. This could not be demonstrated, however, in the 11.5 mm. embryo. The greater portion of the fibers of these trunks passes to the region of the three external gills.

The *truncus visceralis X* (Plate I, *T. Vi. X*) leaves the posterior extremity of the visceral X ganglion and extends ventro-caudad. A very short distance beyond the ganglion a lateral branch (Plate I, *T. Vi. X. 1*) leaves the trunk and extends latero-caudad to the region of the third external gill. The main portion of the trunk continues ventro-caudad and comes into close relations with the alimentary canal in the region posterior to the gills. A portion at least of its fibers may be traced to the epithelium of the alimentary canal in this region.

Dorsal Lateralis X Ganglion.

This ganglion (Plate I, *G. D. L. X*) lies throughout its whole extent dorsal to the visceral X, and posteriorly becomes in some individuals partially fused with it (Plate III, Fig. 9; Plate IV, Fig. 9a). Its anterior end is at about the transverse level of the visceral X root; its posterior end about as far caudad as the posterior end of the visceral ganglion. In early stages it is quite separate from the ventral lateralis X, but in the 11.5 mm. embryo the latter has become fused with a portion of its ventro-lateral border. (Plate III, Fig. 9; Plate IV, Fig. 9a).

The root of the dorsal lateralis X ganglion has been described above as the most posterior portion of the lateralis IX and X root. (See pp. 241 and 242).

But one ramus leaves the dorsal lateralis X ganglion, the *ramus lateralis superior X* (Plate I, *R. L. s. X*), which is purely lateralis in character. It arises from the posterior extremity of the ganglion and extends directly caudad. A short distance beyond the ganglion a branch is given off dorsally (Plate I, *R. L. s. d. X*), which after ascending a little continues caudad more or less parallel with the main portion of the ramus. Both portions supply lateral line organs along the dorsal portion of the side of the body.

Ventral Lateralis X Ganglion.

Up to the present time two lateralis ganglia on X have been definitely described for Amphibia only by Landacre and McLellan in the embryo of Rana. The more general relations of the ventral lateralis X ganglion in that form are almost exactly the same as those of the ganglion to which I have given that name in the embryo of Ambystoma. (Plate I; Plate III, Figs. 7, 8, and 9; Plate IV, Figs. 7a, 8a, and 9a; *G. V. L. X*).

In all the stages studied, this ganglion lies in contact with the dorso-lateral surface of the visceral X ganglion; and this contact is maintained usually throughout its whole length. In the later stages studied it is usually fused more or less completely with the dorsal lateralis IX ganglion and the ventral border of the dorsal lateralis X. In early stages, however, it is uniformly quite distinct from both of these. In the 11.5 mm. embryo from which the reconstruction was made, the process of fusion had gone farther on one side of the body than on the other. On the right side, which was plotted, the ventral lateralis X ganglion, while close to lateralis IX, was quite separate from it; on the left side the two had come into contact, though the limits of each were still recognizable. On both sides of the body the dorsal and ventral lateralis X ganglia were already partly fused. (Plate I; Plate III, Fig. 9; Plate IV, Fig. 9a).

In its anterior portion the ventral lateralis X ganglion extends much farther dorsad than it does farther back, its dorsal border rising to the level of the root of the dorsal lateralis X ganglion, and lying just lateral to it. (Plate I; Plate III, Fig. 7; Plate IV, Fig. 7a). At no point in this region, however, is there the least indication of fusion or connection with this root. Just below this root the ganglion is in contact with a portion of the lateral border of the cutaneous ganglion. This anterior portion of the ventral lateralis ganglion comprises, in most specimens, the greater portion of its bulk. Just posterior to the point of origin of the second branchial trunk, the ganglion becomes perceptibly smaller, sometimes dwindling away to a mere layer only a cell or two in thickness, closely applied to the surface of the visceral ganglion. Occasionally beyond this point it seems to disappear completely for a few sections. This suggests the idea that it may consist primitively of two ganglia, one anterior, the other posterior. To settle this point further study is necessary.

It may be noted here that all of the lateralis ganglia, in VII, IX, and X, invariably lie lateral to any other ganglia that may happen to be in the same horizontal plane with them. A glance at the reconstruction (Plate I) will make this evident. The same thing is true of the lateralis ganglia in the embryo of Rana, as shown by the reconstructions accompanying the paper of Landacre and McLellan.

No separate root of the ventral lateralis X ganglion could be found in any of the stages studied. Although, as stated above, the ganglion comes into close proximity to the dorsal lateralis root, no fibers pass from it to this root in this region. It is noteworthy that in the embryo of Rana, likewise, no separate root of the ventral lateralis X ganglion was found.

From the posterior end of the ventral lateralis X ganglion arises the lateralis component of the visceral trunk, the *ramus lateralis inferior* (Plate I, *R. L. i. X*), which passes ventro-caudad in company with the remaining components of the visceral trunk. In most transverse sections it is extremely difficult to be certain of the presence of this component in even the most proximal portion of the trunk. In parasagittal sections, however, the relation of its fibers to the cells of the ventral lateralis ganglion is absolutely unmistakable.

In the region of the origin of the branchial trunks from the visceral ganglion, the ventral lateralis ganglion presents very strongly an appearance of contributing fibers to these trunks, and this appearance is given added force by the large size of the ganglion in this region, coupled with the fact that no other ramus arises from this portion. It is true that the relations here are confused by the fact that fibers of another component, either cutaneous or motor (possibly both), passing down from the cutaneous ganglion, and then between the ventral lateralis and visceral ganglia, enter the branchial trunks at this point. Nevertheless, the appearance mentioned is too striking and too definite to be explained entirely as due to confusion with these other fibers.

But, in spite of repeated and most careful study of this point, I have not succeeded in tracing fibers from the branchial trunks to unmistakable lateral line organs. Moreover, Coghill found no lateralis fibers in these trunks in the late larval stage of Ambystoma, and, to the best of my knowledge, they have not been described as present there in any other form, either among fishes or Amphibia.

What, then, is the significance of this rather large mass of cells making up the anterior and larger portion of what I have called the ventral lateralis ganglion? One possibility that naturally occurs to one is that this ganglion actually sends lateralis fibers into the branchial trunks in the embryo, but that this is merely a rudimentary and transitory condition, disappearing by the time the late larval stage is reached. I am forced to say that, considering all the relevant facts, this hypothesis does not seem a very probable one. Another, and even more extreme possibility, is that this group of cells is not part of the lateralis system at all; that it is, perhaps, a special visceral ganglion, which sends gustatory fibers down the branchial trunks to innervate taste-buds in the region of the gills. It will be recalled that the cells comprising the most ventral portion of the ventral lateralis IX ganglion similarly give the appearance of sending fibers into the glossopharyngeal trunk, where I have not been able to demonstrate the presence of lateralis fibers by following the distribution, and where, likewise, they have never been found in other vertebrates.

Strong evidence against the possible special visceral character of these portions of the ventral lateralis IX and ventral lateralis X ganglia is afforded by their histological character. (See p. 252). The lateralis ganglia in general present the most distinctive appearance of any of the components, largely due to the uniformly larger size, rounded form, and lighter staining reaction of their cell nuclei. In these and all other respects that I have noted, the questionable portions of the two ganglia under discussion are absolutely indistinguishable from any other portions of any of the lateralis ganglia. In the few cases where special visceral ganglia have been definitely identified in embryonic stages, as in Ameiurus (Landacre, 1910) and in Lepidosteus (Landacre, 1912), their histological appearance has been unmistakably different from that of the lateralis ganglia.

It is interesting to note that a number of rather small lateral line organs are present on the operculum, close to the bases of the gills; but, while fibers from the branchial trunks can be readily followed to this general region, and pass in close proximity to these lateral line organs, I have not been able to trace them to the organs with certainty.

Motor X component. The motor component of X leaves the medulla by several areas of exit. A portion of the fibers leave the medulla just ventral to the area of entry of the large cutaneous and visceral root; the rest by three other areas of exit, at about the same level, and posterior to this point. The fibers from these posterior areas of exit pass forward to the visceral and cutaneous root, and are soon indistinguishable among its fibers. Their further distribution was not studied.

Histological Characters of the Ganglia.

The nuclei of the cells of the cranial ganglia, in the preparations studied, stand out for the most part with great distinctness. The chromatin is not collected largely in a central nucleolus, as is the case in the embryo of Rana, but is distributed rather uniformly throughout the nucleus. (Compare detail drawings, Plate IV, with similar drawings accompanying Landacre and McLellan's paper on Rana.) The limits of the cytoplasm of the individual cells it is usually impossible to make out, at least within the ganglia. It is apparent, therefore, that any histological differentiation between the different ganglia that we may be able to recognize must be largely a matter of the appearance of the nuclei of the cells.

The size, shape, and depth of staining of the nuclei in a given ganglion, or in the ganglia belonging to a given system (cutaneous, lateralis, etc.) varies considerably. Nevertheless, this variation in a given case has its limits, as far as any considerable number of the nuclei are concerned, and, with the exception of cases which will be discussed below, the ganglia of a given system have a fairly uniform appearance.

In the 11.5 mm. embryo the most striking contrast in histological appearance between different ganglia is that between the lateralis ganglia and all the others. The nuclei of the cells of the lateralis ganglia are larger and rounder, and do not stain as heavily with Delafield's hæmatoxylin as do the nuclei of other ganglia. (See Plate IV, Figs. 1a, 2a, 3a, 5a, 6a, 7a, 8a, and 9a). They thus stand out in strong contrast, and even when the lateralis ganglia are practically fused with other ganglia, the limits of each are readily recognized by reason of these differences.

In stages younger than the 11.5 mm. embryo, these differences become less pronounced, and in the earliest stage where the ganglia are distinctly recognizable, can hardly be detected. The degree of contrast varies also in different specimens to a very great extent, due probably, largely if not entirely, to differences in fixation, staining, etc.

Between the cutaneous and visceral ganglia it is harder to detect differences of histological appearance. On the whole, the nuclei of the visceral ganglia seem to stain a little heavier than those of the cutaneous ganglia, for the most part are packed together a little closer, and perhaps average a trifle smaller. The variation is considerable, however, and sections can be found showing exactly the reverse condition.

Of the two regions of the auditory ganglion spoken of on page 239, the nuclei in the more anterior and dorsal region are very slightly larger, slightly lighter-staining, and not packed quite so close together as those in the ventro-posterior portion. These differences are exceedingly slight in the 11.5 mm. embryo; in the oldest of the early larval stages studied they have become much more pronounced, and the contrast between the two regions of the ganglion is very striking.

In the earlier embryonic stages studied two kinds of coloring material are present in the cytoplasm of the ganglion cells: yolk granules and pigment granules. The latter, as seen under the 4 mm. objective, are mere specks, of a brownish color, and identical in appearance with the pigment granules visible at the same time in the cells of the ectoderm. The yolk granules are larger, of various shapes, and stain much like the cytoplasm itself—usually a little darker. As development proceeds these yolk granules are apparently absorbed; in the 11.5 mm. embryo they are no longer present in the ganglion cells, though still numerous in muscle and loose mesenchyme cells. At the same time the pigment granules undergo changes. In the 11.5 mm. embryo the lateralis ganglia are for the most part well pigmented, but the pigment, now of a yellowish-brown color, is uniformly spread through the cytoplasm of the cells, and the individual granules are not visible under the 4 mm. objective. In the other ganglia, the pigment is almost entirely absent. This furnishes another means by which, in many preparations, the lateralis ganglia are readily distinguished from the others.

SUMMARY.

In late larval and adult stages of urodeles the ganglia of the cranial nerves are usually closely fused into three ganglionic masses. To learn the primary relations of the individual ganglia of these nerves, embryonic stages must be studied in which this fusion has not yet taken place, or in which it has not proceeded very far. The descriptions in this paper are of such stages.

In the 11.5 mm. embryo of Ambystoma jeffersonianum, the more general relations of the ganglia of the V and VII nerves are essentially the same as reported by Coghill in the late larval stage of Ambystoma tigrinum.

The Gasserian or cutaneous V ganglion lies close to the lower portion of the anterior end of the medulla, in the region between the optic and auditory vesicles. At this stage a separate profundus portion can not be distinguished in the Gasserian, but this distinction is very marked in the earlier stages.

The dorsal lateralis VII ganglion lies dorsal to the Gasserian ganglion.

The geniculate or visceral VII ganglion is posterior to the Gasserian, and except for its most ventral portion, lies in the space between the auditory vesicle and the medulla.

The ventral lateralis VII ganglion lies under the anterior end of the auditory vesicle, ventro-laterad of the geniculate ganglion, to which its proximal end is fused.

Only a single auditory ganglion could be recognized, in which, however, two different regions could be distinguished. These are characterized by histological differences, which are much more marked in the later stages studied.

In essential features the IX-X complex in the 11.5 mm. embryo is similar to that reported by Landacre and McLellan in Rana.

The visceral IX ganglion (G. petrosum) is quite separate from the visceral X; it lies just posterior to the auditory vesicle.

In earlier stages two distinct lateralis ganglia are present on IX, one of which gives rise to the ramus supratemporalis, the other to the lateralis component of the ramus auricularis. In the 11.5 mm. embryo these have united; the combined ganglia lie dorsal to the visceral IX.

Of the ganglia of X, the cutaneous or jugular is most mesial, and is close to the medulla. The cutaneous component of the ramus auricularis was the only component from it that was recognized with certainty, but its large size makes it probable that it sends components to other nerves as well.

The visceral X ganglion (G. nodosum) has a position posterior to the visceral IX and lateral to the cutaneous X. In stages earlier than the 11.5 mm. embryo it is divided by a constriction in its middle part into two portions, the more anterior giving rise to the two branchial trunks, the more posterior to the visceral trunk.

As in all the other urodeles hitherto studied, all the root fibers from the lateralis ganglia of IX and X unite into one large common root before entering the medulla. The area of entry of this root is the most anterior of all the roots of IX and X, being slightly farther cephalad than the visceral root of IX.

The dorsal lateralis X ganglion lies dorsal to the visceral X ganglion.

The ventral lateralis X ganglion lies throughout its extent in close contact with the dorso-lateral surface of the visceral X ganglion. In the 11.5 mm. stage it is partially fused with the ventral border of the dorsal lateralis X ganglion; later it becomes fused with dorsal lateralis IX also. No separate root of this ganglion could be identified.

The greater bulk of the ventral lateralis X ganglion is in the region of the branchial trunks, and it has here the appearance of contributing fibers to these trunks. Whether this is actually the case could not be definitely settled; our knowledge of the character of the branchial trunks in late larval stages of Ambystoma and other forms would not lead us to expect to find lateralis fibers in them in the embryo. The character of this anterior portion of the ganglion is not considered definitely settled.

Except in the earliest embryonic stages, the nuclei of the cells of the lateralis ganglia are uniformly larger, rounder, and lighter-staining (with Delafield's hæmatoxylin) than those in the other ganglia. The differences between the nuclei of cutaneous and visceral ganglia are slight and not constant.

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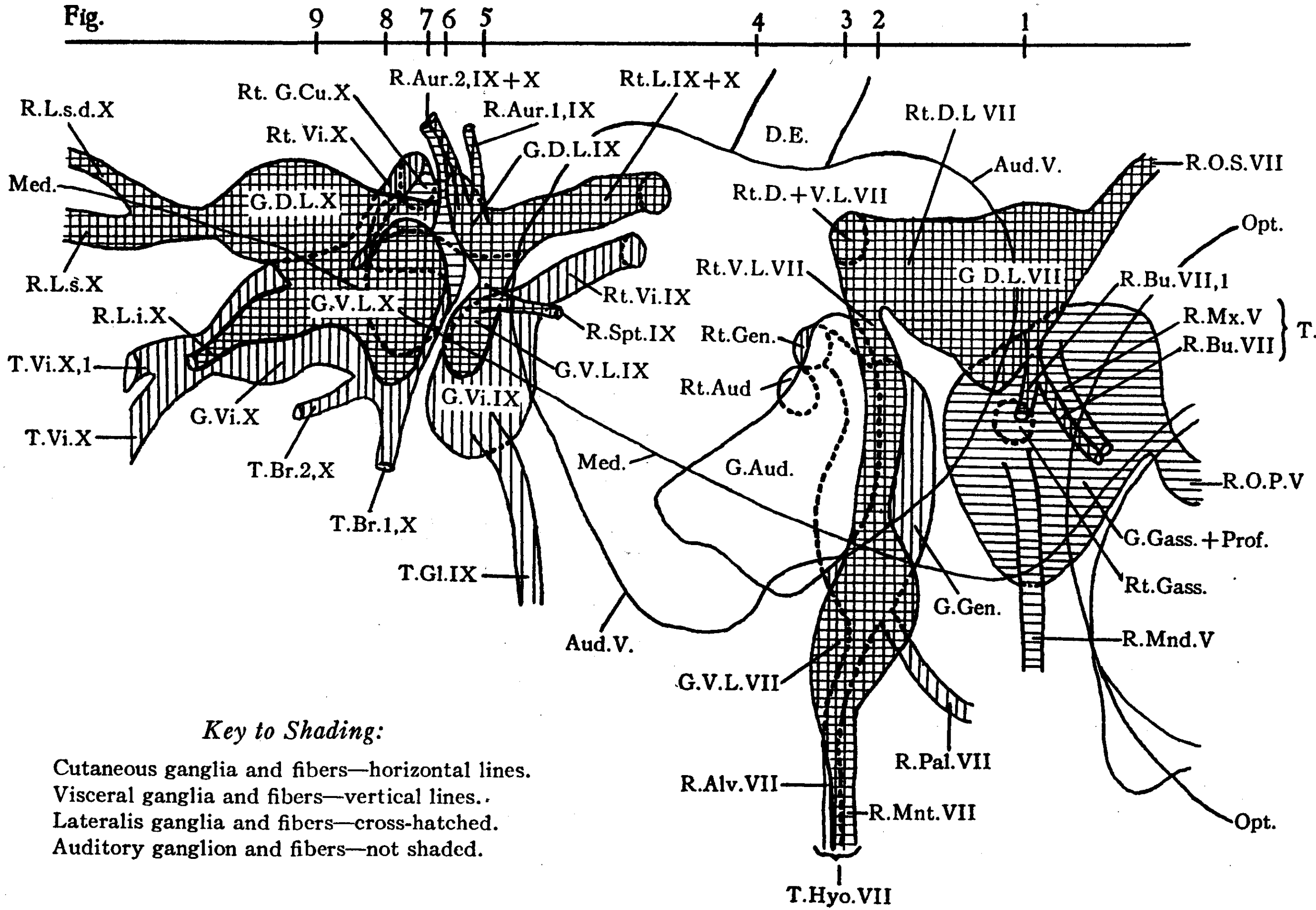
PLATE I.

A reconstruction of the cranial ganglia of an 11.5 mm. embryo of Ambystoma jeffersonianum, being a projection of these ganglia (from the right side of the head) upon the median, vertical plane of the head. The roots of the ganglia and the proximal portions of the chief nerves are shown, but motor components are omitted. The auditory vesicle, part of the optic vesicle, and the base of the brain are shown in outline. The areas of entry of the sensory roots into the medulla are indicated. Above the reconstruction are shown the positions of the sections figured in the following plates. Magnification, × 150.

ABBREVIATIONS.

Aud. V.—outline of auditory vesicle.
B. V.—blood vessel.
D. E.—ductus endolymphaticus.
En.—outgrowth of endoderm from lateral angle of pharynx.
G. Aud.—auditory ganglion.
G. Cu. X—cutaneous X ganglion.
G. D. L. VII—dorsal lateralis VII ganglion.
G. D. L. IX—dorsal lateralis IX ganglion.
G. D. L. X—dorsal lateralis X ganglion.
G. Gass. (+Prof.)—Gasserian ganglion, into which profundus ganglion has been incorporated.
G. Gen.—geniculate ganglion.
G. Vi. IX—visceral IX ganglion.
G. Vi. X—visceral X ganglion.
G. V. L. VII—ventral lateralis VII ganglion.
G. V. L. IX—ventral lateralis IX ganglion.
G. V. L. X—ventral lateralis X ganglion.
H. C.—horizontal canal of auditory vesicle.
M.—muscle.
M. d. m.—depressor mandibulæ muscle.
Med.—medulla; in reconstruction, base of medulla.
M. l. d.—longissimus dorsi muscle.
M. l. d. i.—longissimus dorsi inferior muscle.
M. ma.—masseter muscle.
Mo. VII—motor component of VII.
M. tem.—temporalis muscle.
No.—notochord.
Opt.—outline of optic vesicle.
Pal. B.—palatoquadrate bar.
Par.—parachordal.
Phar.—pharynx.
R. Alv. VII—ramus alveolaris VII.
R. Aur. 1, IX—ramus auricularis 1, IX.
R. Aur. 2, IX+X—ramus auricularis 2, IX+X.
R. Aur.?—branch of auricularis?
R. Bu. VII—ramus buccalis VII.
R. Bu. VII, 1—first branch of ramus buccalis VII.
R. L. i. X—ramus lateralis inferior X.
R. L. s. X—ramus lateralis superior X.
R. L. s. d. X—dorsal branch of ramus lateralis superior X.
R. Mnd. V—ramus mandibularis V.
R. Mnt. VII—ramus mentalis VII.
R. Mnt. VII, 1—first branch of ramus mentalis VII.
R. Mx. V—ramus maxillaris V.
R. O. S. VII—ramus ophthalmicus superficialis VII.
R. O. P. V—ramus ophthalmicus pro. fundus V.
R. Pal. VII—ramus palatinus VII.
R. Sac. VIII—ramus acusticus sacculi.
R. Spt. IX—ramus supratemporalis IX.
R. Utr. VIII—ramus acusticus utriculi.
Rt. Aud.—root of auditory ganglion.
Rt. Cu. X—root of cutaneous X ganglion.
Rt. D. L. VII—root of dorsal lateralis VII ganglion.
Rt. D.+V. L. VII—root of dorsal and ventral lateralis ganglia of VII.
Rt. Gass.—root of Gasserian ganglion.
Rt. G. Cu. X—cutaneous X root and ganglion.
Rt. Gen.—root of geniculate ganglion.
Rt. L. IX+X—lateralis root of IX and X.
Rt. L. X—lateralis root of X.
Rt. Mo. X—motor root of X.
Rt. Vi. IX—root of visceral IX ganglion.
Rt. Vi. X—root of visceral X ganglion.
Rt. V. L. VII—root of ventral lateralis VII ganglion.
T. Br. 1, X—truncus branchialis 1, X.
T. Br. 2, X—truncus branchialis 2, X.
T. Gl. IX—truncus glossopharyngeus IX.
T. Hyo. VII—truncus hyomandibularis VII.
T. Inf. V+VII—truncus infra-orbitalis V+VII.
T. Vi. X—truncus visceralis X.
T. Vi. X, 1—first branch of truncus visceralis X.



Key to Shading:

Cutaneous ganglia and fibers—horizontal lines.
Visceral ganglia and fibers—vertical lines.
Lateralis ganglia and fibers—cross-hatched.
Auditory ganglion and fibers—not shaded.

PLATE II.

(Shading as in Plate I; in addition, motor components in solid black.)

Fig. 1. A camera outline drawing of a portion of a section through the head of an 11.5 mm. embryo of Ambystoma jeffersonianum. The section passes through the dorsal lateralis VII ganglion (*G. D. L. VII*) and the Gasserian ganglion (*G. Gass.*). The position of this section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 1a.

Fig. 2. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the geniculate (*G. Gen.*) and ventral lateralis VII (*G. V. L. VII*) ganglia. The junction of the roots of the dorsal and ventral lateralis VII ganglia is shown. The position of this section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 2a.

Fig. 3. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the geniculate (*G. Gen.*), auditory (*G. Aud.*), and ventral lateralis VII (*G. V. L. VII*) ganglia. The position of this section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 3a.

Fig. 4. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the posterior part of the auditory ganglion (*G. Aud.*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 4a.

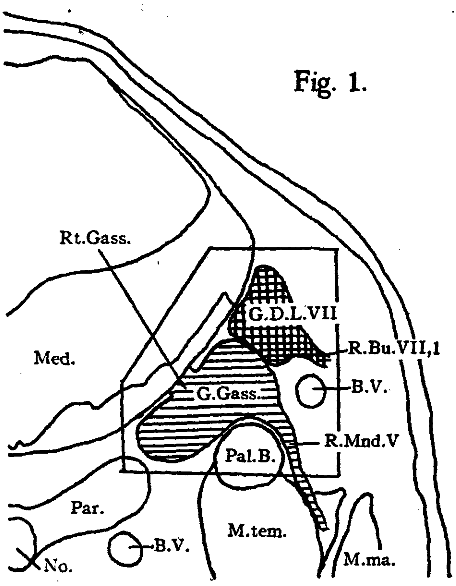


Fig. 1.

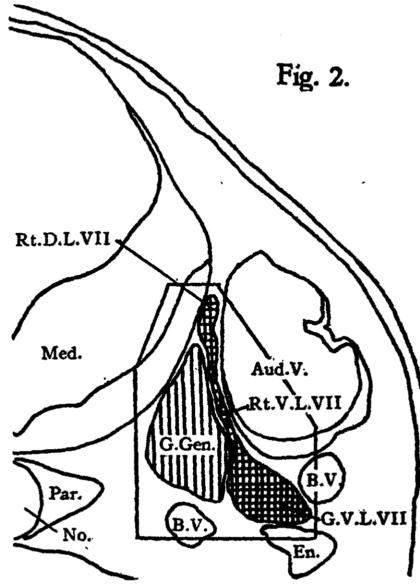


Fig. 2.

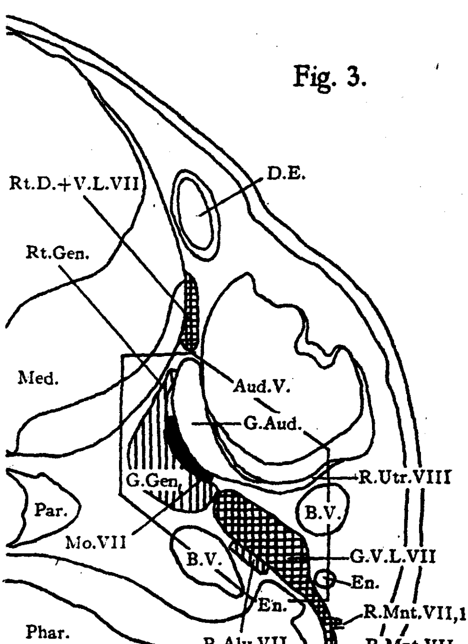


Fig. 3.

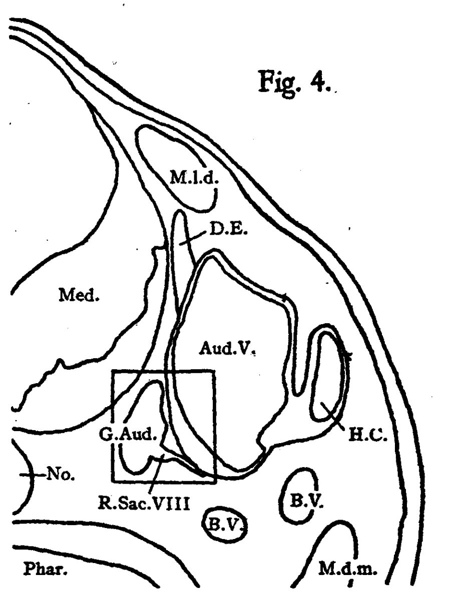


Fig. 4.

PLATE III.

(Shading as in Plate I; in addition, motor components in solid black.)

Fig. 5. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo of Ambystoma jeffersonianum. The section passes through the ventral lateralis IX ganglion (*G. V. L. IX*) and the visceral IX ganglion (*G. Vi. IX*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 5a.

Fig. 6. A camera outline drawing of a portion of a section through the head of an embryo of Ambystoma jeffersonianum, slightly older than the 11.5 mm. stage from which all the remaining drawings and the reconstruction were made. The section passes through both dorsal and ventral lateralis IX ganglia (*G. D. L. IX; G. V. L. IX*); through the visceral IX ganglion (*G. Vi. IX*); the cutaneous X ganglion (*G. Cu. X*); and through the root of the dorsal lateralis X ganglion (*Rt. L. X*). The position of the corresponding section of the 11.5 mm. embryo in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 6a. (The relationship of lateralis and cutaneous components of the ramus auricularis could not be well shown in any one section of the 11.5 mm. embryo from which all the remaining drawings were made.)

Fig. 7. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo of Ambystoma jeffersonianum used in making all drawings except Figs. 6 and 6a. The section passes through the cutaneous X ganglion (*G. Cu. X*); the root of the dorsal lateralis X ganglion (*Rt. L. X*); the ventral lateralis X ganglion (*G. V. L. X*); the visceral X ganglion (*G. Vi. X*); and the visceral IX ganglion (*G. Vi. IX*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 7a.

Fig. 8. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the cutaneous X ganglion (*G. Cu. X*); the ventral lateralis X ganglion (*G. V. L. X*); and the visceral X ganglion (*G. Vi. X*); also through the anterior tip of the dorsal lateralis X ganglion (*G. D. L. X*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 8a.

Fig. 9. A camera outline drawing of a portion of a section through the head of the same 11.5 mm. embryo. The section passes through the visceral X ganglion (*G. Vi. X*) and the fused dorsal and ventral lateralis X ganglia (*G. D. L. X* and *G. V. L. X*). The position of the section in relation to the reconstruction on Plate I is indicated at the top of that plate. Magnification, × 80. The details of the area blocked out are shown in Plate IV, Fig. 9a.

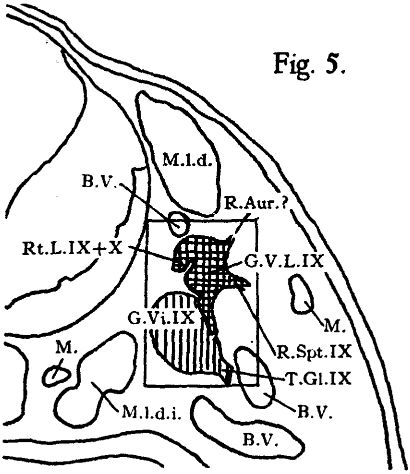


Fig. 5.

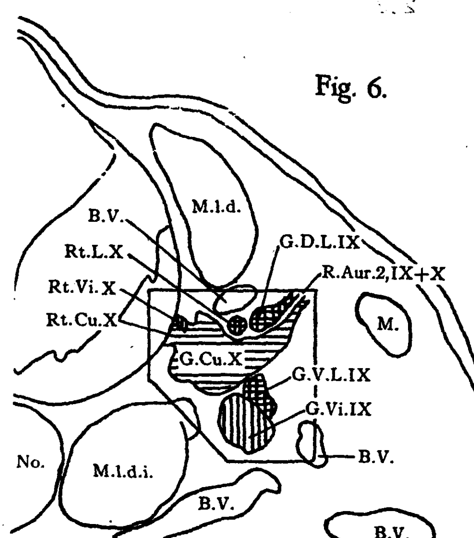


Fig. 6.

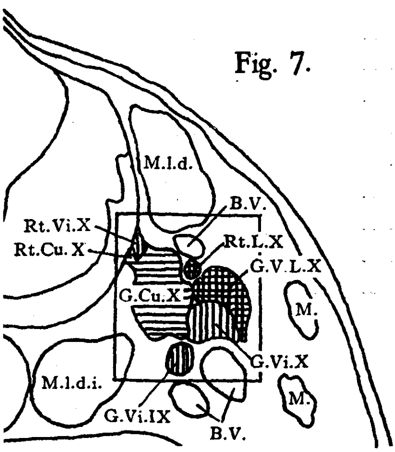


Fig. 7.

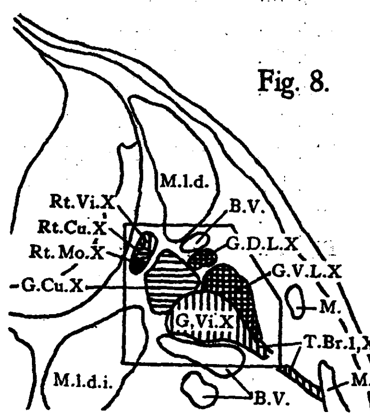


Fig. 8.

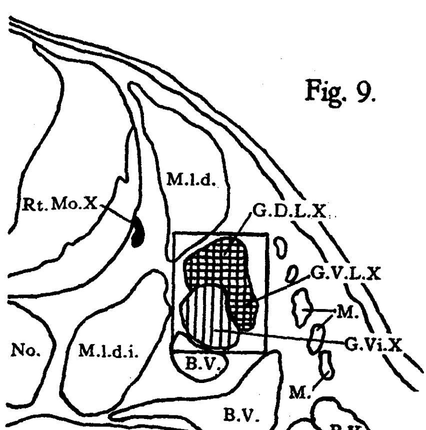


Fig. 9.

PLATE IV.

Fig. 1a. Details of area blocked out in Fig. 1. Magnification, × 132.
Fig. 2a. Details of area blocked out in Fig. 2. Magnification, × 132.
Fig. 3a. Details of area blocked out in Fig. 3. Magnification, × 132.
Fig. 4a. Details of area blocked out in Fig. 4. Magnification, × 132.
Fig. 5a. Details of area blocked out in Fig. 5. Magnification, × 132.
Fig. 6a. Details of area blocked out in Fig. 6. Magnification, × 132.
Fig. 7a. Details of area blocked out in Fig. 7. Magnification, × 132.
Fig. 8a. Details of area blocked out in Fig. 8. Magnification, × 132.
Fig. 9a. Details of area blocked out in Fig. 9. Magnification, × 132.

Fig. 1a.

Fig. 4a.

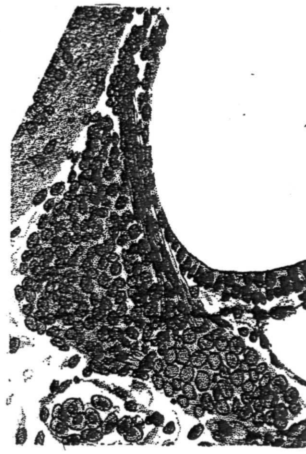


Fig. 2a.

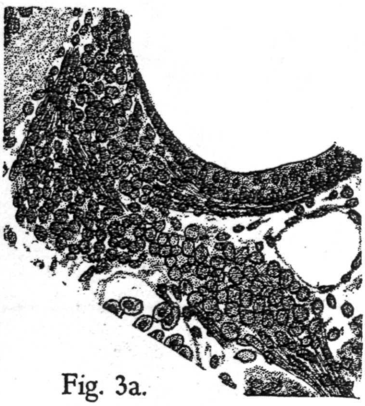


Fig. 3a.

Fig. 5a.

Fig. 6a.

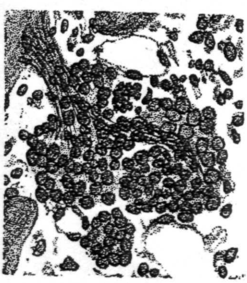


Fig. 7a.

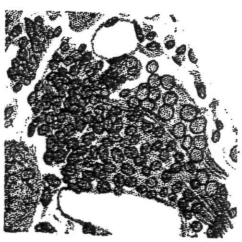


Fig. 8a.

Fig. 9a.